The dawn of a dynasty: life strategies of Cambrian and Ordovician brachiopods

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Brachiopods are among the first animal phyla to emerge from the Cambrian Explosion, rapidly diversifying to all major palaeocontinental blocks within 20 million years. The group underwent another steep diversification during the Ordovician and their relative abundance and diversity made them one of the most successful invertebrate groups during the entire Palaeozoic. During this time brachiopods lived in a range of environments, and represented a significant component of marine ecosystems, yet information regarding their modes of life and ecology is somewhat limited. Recent studies, primarily from the Chengjiang and Burgess Shale Lagerstätten have revealed that by the middle Cambrian (Series 3, Stage 5) brachiopods from across the phylum had already developed a range of ecological strategies and life modes. Cambrian brachiopods occupied distinct trophic niches on soft and hard substrates and exhibited at least five types of lifestyles: pedicle attachment, pedicle anchoring, cemented, free lying and semi-infaunal. Comparisons with Ordovician benthic assemblages show that despite the explosion of brachiopod taxa witnessed in the Ordovician, with the exception of the appearance of

burrowing brachiopods, life strategies of brachiopods remained largely the same. Indicating that the majority of life modes observed in brachiopods had rapidly evolved and was already in place prior to the Great Ordovician Biodiversity Event.

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Brachiopods are a group of exclusively marine, bivalved invertebrates that globally constitute only a minor component of modern marine communities. Despite their modest present-day diversity (Emig *et al.* 2013), brachiopods have been one of the most successful marine phyla with a history that spans over 500 million years. The group was one of the first metazoan organisms to secrete a biomineralized shell (Pelman 1977; Ushatinskaya 2008; Topper *et al.* 2013a; Skovsted *et al.* 2015), rapidly establishing themselves as a significant and widespread component of Cambrian communities (Holmer *et al.* 1996; Brock *et al.* 2000; Ushatinskaya 2008). Although, the group was conspicuous in Cambrian communities, it was the unprecedented hike in diversity, particularly at the family, genus and species taxonomic levels during the Ordovician that established brachiopods as an integral component of the Palaeozoic

benthic realm. This taxonomic expansion in the Ordovician is reflected in the advent of a range of different shell shapes, as brachiopods sought to exploit a range of new ecological opportunities within the benthos (Harper 2006, 2010; Harper *et al.* 2013).

Their abundance and possession of a biomineralized shell have endowed brachiopods with one of the most complete fossil records of any phyla (Sepkoski 1981), however the large majority of taxa are known almost exclusively from their shell morphology. The rarity of preserved soft-tissues has left substantial gaps in our knowledge regarding their mode of life and ecological interactions with other organisms and their surrounding environment. Despite what is seen as an apparently simple and relatively conservative ground plan (Kowaleski *et al.* 1997; Krause 2004), brachiopods have developed an extraordinary diversity of morphological skeletal forms and studies generally attributed this variability to the diverse range of life modes and environments that brachiopods inhabit (Thayer & Steele-Petrovic 1975; Alexander 1977, 1984; Thayer 1981; James *et al.* 1992). On the basis of shell morphology, many researchers have established the lifestyles of fossil brachiopods through the interpretation of morphological data and analogies with living forms (e.g. Ager 1967; Rudwick 1970; Richards 1972; Thayer 1979; Grant 1976; Curry 1983; Bassett 1984; Plotnick *et al.* 2013). Direct fossil evidence of brachiopod life modes is relatively rare, in part due to the dependency of most brachiopods on a taphonomically fragile pedicle for attachment and support. However, over the past few decades a number of Cambrian and Ordovician studies have documented brachiopods in life position allowing a more accurate reconstruction of brachiopod lifestyles in the fossil record.

Here we provide a comparative palaeoecological study of brachiopod lifestyles from the phylum's' emergence in the Cambrian to its subsequent spectacular

radiation in the Ordovician. We concentrate on the direct evidence available on how brachiopods lived, specifically their relationship with substrate and their ecological interactions with other species. Our aim is to investigate whether the explosion of brachiopod diversity in the Ordovician is reflected in a parallel rise in the diversity of brachiopod life strategies giving insights into the role that the Brachiopoda played in some of the earliest animal benthic communities.

The Cambrian Way of Life

Our understanding of the ecology of animals during the crucial Cambrian interval is largely driven by the examination of exquisitely preserved, soft-bodied organisms from Burgess Shale-type deposits. Brachiopods are no exception and the Cambrian Stage 3 Chengjiang Lagerstätte (Zhang *et al.* 2003, 2004, 2005, 2007a, b, c, 2008, 2009, 2011a,b; Zhang & Holmer 2013), the Cambrian Stage 5 Burgess Shale Lagerstätte (Holmer & Caron, 2006; Pettersson Stolk *et al.* 2010; Topper *et al.* 2014, 2015a, b, accepted) and to a lesser extent the Stage 4 Guanshan Biota (Hu *et al.* 2010) have provided much of our knowledge regarding the early ecology and adaptive morphologies of the Brachiopoda. Brachiopods have been documented from other Cambrian Lagerstätten, such as the Kaili Biota (Zhao *et al.* 2005, Mao *et al.* 2016), Emu Bay (Paterson *et al.* 2016) and the Spence Shale (Garson *et al.* 2011) however they are typically bereft of soft parts and offer no or little direct evidence of attachment or lifestyles. Although, a single specimen showing two brachiopods attached to the helens of a hyolith has been recently illustrated from the Spence Shale (Moysiuk *et al.* 2017). The Chengjiang and Burgess Shale deposits yield a highly disparate and low diversity brachiopod fauna (Zhang & Holmer 2013; Topper *et al.*

2015b). Sixteen species from eleven families have been documented across the two localities (excluding the stem-group forms), allowing for an expansive view of life strategies across the phylum (Fig. 1). The exquisite preservation clearly demonstrates that by the mid-Cambrian, not only had the phylum acquired a range of shell and soft-part morphologies but also developed an array of life strategies (Zhang & Holmer 2013; Topper *et al.* 2015b).

The majority of brachiopods are, and probably were, fixosessile organisms, attached to a variety of substrates via a fleshy pedicle (Williams *et al.* 1997; Harper & Moran 1997). However, pedicle morphology varies considerably in different taxa and it is this variation that allows pedunculate brachiopods considerable flexibility in their choice of substrate. For example, some brachiopods in the Chengjiang and Burgess Shale communities are attached to a range of hard substrates, including skeletal debris, conspecific and non-conspecific brachiopods, motile skeletal-bearing organisms, enigmatic tubes, algae, chancelloroids and sponges (Fig. 1). Pedicle morphology varies from attachment via a short, pad-like pedicle (e.g. *Micromitra burgessensis* Resser, 1938, see Topper *et al.* 2015a,b; Fig. 1A,B) to a much thicker and longer (<2 times shell length) pedicle (e.g. *Longtancunella chengjiangensis* Hou, 1999, *Xianshanella haikouensis* Zhang & Han, 2004 and *Alisina* sp., Fig. 1G). Topper *et al.* (2014, 2015a,b) suggested that perhaps one of the most important adaptations of Cambrian brachiopods was the ability to attach to hard substrates and subsequently raising the individuals above the seafloor. The potential evolutionary advantage of hard substrate attachment has been discussed in some length (Zhang *et al.* 2009; Zhang & Holmer 2013; Topper *et al.* 2014, 2015a,b), brachiopods benefiting from ease of attachment, increased food supply, avoidance of turbid benthic conditions, biofoul and possible protection from predators. The ability to attach to hard substrates

also allowed brachiopods to become low and medium secondary tierers (Bottjer & Ausich 1986; Wang *et al.* 2012; Topper *et al.* 2015b), with the ability to exploit different niches in the water column and also partition resources.

Not all pedunculate brachiopods in the Cambrian however, attached to hard substrates and a number of brachiopod species are interpreted as primary tierers with their pedicle entirely or partially buried in sediment for anchorage (Holmer & Caron 2006; Zhang *et al.* 2011a; Zhang & Holmer 2013). These brachiopods typically possess a relatively long (5-7 times shell length) and slim pedicle that bears a bulb-like termination at the distal end (Fig. 1E). The majority of these taxa had lightly mineralized shell valves and may have lived suspended above the turbulent sediment-water interface, tethered by their long, thin pedicles, reminiscent of a kite in the wind (Holmer & Caron 2006; Zhang & Holmer 2013). A similar life strategy has been suggested for the Devonian spiriferid *Austrospirifer* (Blight & Blight 1990) and the widely distributed extant rhynchonellide brachiopod *Cryptopora* (Cooper 1973; Curry 1983). Brachiopods, such as *Diadongia pista* Rong, 1974 and stem group forms, such as *Yuganotheca elegans* have been interpreted as having a semi-infaunal lifestyle with their pedicle entirely buried in sediment with the valves exposed at the sediment-water interface (Zhang *et al.* 2003, 2008; Zhang & Holmer 2013). *Diaongia pista* is also frequently utilized as substrate in the Chengjiang Lagerstätte, notably by *L. chengjiangensis* and a cementing brachiopod *Inquilinus haikouensis* (Han *et al.*, 2004). Specimens of *I. haikouensis* are interpreted as a represented a brachiopod larval stage and are cemented long the anterior and lateral commissure of *D. pista* individuals (Zhang *et al.* 2009, fig. 2).

Despite the exquisite preservation of the Chengjiang fauna, no evidence of a pedicle has been observed in the stem-group brachiopod *Heliomedusa orienta* Sun &

Hou, 1987, a taxon that is generally considered to be related to the more widespread stem group brachiopod, *Mickwitzia* (Skovsted *et al.* 2009; Butler *et al.* 2015). Like *D. pista*, *H. orienta* is frequently utilised as a basibiont attachment substrate for other organisms (Zhang *et al.* 2009) and it is probable that *H. orienta* was a free-lying suspension-feeding member of the benthos (Zhang & Holmer 2013).

The Ordovician Way of Life

The Ordovician witnessed profound changes in the biodiversity and biocomplexity of marine life (Webby *et al.* 2004; Harper et al. 2004; Harper 2006). Associated with continental dispersal, brachiopod diversity escalated, and numerically speaking, taxa increased around carbonate platforms and also expanded into deeper water (Harper 2006, 2010). The occurrence of pedunculate brachiopod in fine-grained, deeper water strata has provided palaeontologists with persistent headaches. A variety of life modes have been presented and perhaps unsurprisingly, attachment to hard substrates is interpreted as being crucial for the survival of many brachiopod groups. For example, Gabbott (1999) documented orthocones from the Soom Shale Lagerstätte in South Africa with hundreds of epibiont orbiculoid brachiopods attached and Carrera (2000) illustrated specimens of *Platystrophia* and *Orthidium* attached to sponges in the Early Ordovician of Argentina.

One of the most spectacularly preserved specimens was described by Sandy (1996), from the Upper Ordovician of Ohio. The single specimen comprises over 60 individuals of the atrypid species, *Zygospira modesta* (Say in Hall, 1847) attached via a pedicle to the stem of a crinoid. The brachiopods circumnavigate the crinoid column (Sandy 1996, fig. 1) and are interpreted as colonizing the crinoid stem *in vivo*. The

genus, *Zygospira* has also been documented attached to a cluster of cornulitids that in turn is attached to the stem of a crinoid (Morris & Felton 2003). According to Sandy (1996) this brachiopod-crinoid relationship is not rare (extending to the Carboniferous, see Schneider 2003), however published examples are few. Pedunculate brachiopods have also been documented attached to bryozoans in the Upper Ordovician of Ohio (Richards, 1972) and the mid Ordovician of Canada, where over 30 individuals of *Onniella* are attached to an arborescent trepostome bryozoan (Harper & Pickerill 1996, Fig. 2). Brachiopods attaching to other brachiopods is a lifestyle preserved among Cambrian communities (e.g. *M. burgessensis* and *L. chengjiangensis*, see Zhang *et al.* 2011a; Topper *et al.* 2015a, b) however it is not until the Tremadocian that brachiopod-pedicle etching traces, known as *Podichnus* are documented (Bromley & Surlyk 1973; Bromley & Heinberg 2006; Santos *et al.* 2014). Santos *et al.* (2014) recorded this ichnogenus on the valves of three brachiopod species from Argentina and attributed these etchings to orthid brachiopods (most likely *Lipanorthis*). The Ordovician also witnessed the emergence of cementing forms such as *Craniops* (Popov & Holmer 2000) and encrusting taxa such as *Petrocrania* (Richards 1972; Bassett 2000).

Attaching to hard substrates was not the only life strategy that existed during the Ordovician and some brachiopods adapted to living on fine-grained sediments by atrophying their pedicles and pursuing a life without peduncular support. Foremost among these soft-sediment brachiopods were the strophomenids, a group that possessed a flattened, concavo-convex shell and lay unattached on the seafloor. Although adapted for, strophomenids are by no means restricted to muddy seafloors with particular genera, such as *Rafinesquina* often preserved in mudstones (Dattilo *et al.* 2008) and shelly limestones (Dattilo *et al.* 2009). Their large, flat shells certainly

aided stability and prevented submersion, however their precise life orientation and degree of facultative motility is still a matter of debate (Rudwick 1970; Richards 1972; Alexander 1975; Thayer 1975; Dattilo 2004; Leighton 2005; Dattilo *et al.* 2009; Plotnick *et al.* 2013).

The rarity of brachiopod soft-part preservation in the Ordovician has impeded recognizing brachiopods that anchor their pedicle in the sediment. However, lingulate brachiopods have been reported from the Ordovician of Wales that display a slim, bulb-terminating pedicle that is comparable to Cambrian anchoring forms (Botting *et al.* 2015). An anchored lifestyle is also frequently shown in palaeoecological reconstructions (McKerrow 1978; Harper 2006; Carrera 2000; Waisfeld *et al.* 2003; Santos *et al.* 2014) and has been suggested for a range of brachiopod genera (Richards 1972; Curry 1981) and it is probable that the lifestyle was common amongst Ordovician taxa. A number of brachiopod taxa, such as *Tritoechia* and *Productorthis* are interpreted as living semi-infaunally, with a reduced pedicle and their umbo submerged in sediment (Waisfeld *et al.* 2003).

Members of the Siphonotretoidea, such as *Acanthambonia* grew spines that may have supplemented the pedicle, possibly assisting the anchoring process of the individual to algal strands above the sea floor (Wright & Nõlvak 1997). This algal-brachiopod association has been documented on occasion and it has been suggested that some brachiopods may have adopted an epiplanktic life mode (Havlíček 1967; Bergström 1968). This has however been questioned (Sheehan 1977) and the exact function of these hollow spines in siphonotretids is uncertain and an alternative explanation is that they functioned to screen coarser particles from entering the mantle cavity (Wright & Nõlvak 1997). Infaunal strategies were also adopted early in the Ordovician by linguliformean brachiopods, a lifestyle that in this subphylum

continues to the present day. *Leontiella* sp. documented from the Floian of China by Balinski & Sun (2013) represents the oldest definitive infaunal brachiopod. *Leontiella* sp. possesses a streamlined shell, burrowing shell sculpture and an almost identical pedicle to its' recent burrowing relatives (Emig 1997), reinforcing its interpretation as an infaunal organism.

Cambrian-Ordovician comparisons and the ecospace flat iron

During a protracted interval of some 40 million years in the mid Ordovician, a massive biodiversity hike would irreversibly change the ocean seafloors. Brachiopods at a generic level went from only four genera in Cambrian Stage 10 (although the grouped had approximately 100 genera in Cambrian Stage 4-5, Paleobiology Database: https://paleobiodb.org) to over 200 by the middle Sandbian (Harper *et al.* 2013). Despite this massive increase in diversity, the lifestyles of brachiopods barely changed. Both Cambrian and Ordovician brachiopods show similar types of substrate relationships, including epifaunal lifestyles via pedicle attachment, pedicle anchoring, free lying on the seafloor and cementation, in addition to semi-infaunal pedicle anchoring strategies. The notable exception is the emergence of an infaunal strategy amongst linguliformean stocks in the Ordovician. It has been suggested on numerous occasions that the Ordovician Radiation was rooted in the Cambrian and is an extension of the Cambrian Explosion (Harper 2006; Harper 2010; Harper *et al.* 2015). It appears that not only were the majority of body plans established before diversifications at lower taxonomic levels took place (Harper 2006; Harper 2010; Harper *et al.* 2015), but also life strategies, at least in the Brachiopoda (Figs 3-4).

To assist in the visualization of brachiopod life strategies a theoretical ecospace 'flat iron' (named after the New York building, due to its thin width relative to height) has been constructed. Based on the ecospace cube designed by Bambach *et al.* (2007; also see Bush *et al.* 2007; Mondal & Harries 2016) the ecospace flat iron has been designed specifically for the Brachiopoda. As all brachiopods are suspension feeders, the 'Feeding' axis has been replaced by 'Attachment strategies' (Fig. 3, Table 1) and the motility axes has been somewhat reduced. Despite the changes, the concept remains the same: to evaluate how many of the potential modes of life that could exist for the Brachiopoda were actually present in a particular regional or temporal framework. To reconstruct brachiopod ecologic parameters, publications establishing the palaeoecologic interpretations of various brachiopod genera have been investigated and allocated on a presence/absence system. We focus on the direct evidence for lifestyles, specifically those discussed above. Parameters are classified on a when the brachiopods are in their adult stage. For example, strophomenids such as *Rafinesquina*, are treated as 'Unattached' despite potentially being attached in the larval stage. Given the range of constraints on a specific clade's morphologic diversity, only a relatively limited proportion of these possible ecospace combinations are actualized. For example, it would be challenging to imagine an unattached, non-motile brachiopod to be elevated in the water column. Some ecospace combinations (such as clasping and co-supportive attachments) are present in post-Ordovician faunas (Harper & Moran, 1997; Richardson 1997; Emig 1997) and will not be dealt with here.

The large majority of brachiopods in the Cambrian and Ordovician were epifaunal taxa attached to hard substrates via a pedicle (Fig. 4). Brachiopods from the Chengjiang and Burgess Shale communities are attached to a range of hard substrates

(Zhang & Holmer 2013; Topper *et al.* 2015b) and although in the Ordovician, attachment substrate may have varied (now predominantly crinoids, bryozoans and cornulitids rather than hyoliths, trilobites and sponges), the strategies for rhynchonelliformean brachiopods are largely the same. Cambrian brachiopods were predominantly low level epifaunal tierers, however a few taxa can be classed as medium level secondary tierers, elevating themselves above 5 cm from the sediment-water interface (Bottjer & Ausich 1986; Wang *et al.* 2012; Topper *et al.* 2015b). Tiering height for Ordovician brachiopods is difficult to ascertain, due to the lack of detailed studies, however the fragmentary crinoid stem colonized *in vivo* by *Zygospira* is 9 cm long (Sandy 1996), suggesting that higher tiering levels were reached in the Ordovician.

Partially or entirely burying the pedicle in sediment for anchorage, was an important adaptation for brachiopods in the Cambrian living in soft-sediment environments (Holmer & Caron 2006; Stolk *et al.* 2010; Zhang & Holmer 2013). Anchoring your pedicle and living suspended above the sediment-water interface or living semi-infaunally are life strategies that continued into the Ordovician (McKerrow 1978; Curry 1981; Waisfeld *et al.* 2003; Santos *et al.* 2014; Botting *et al.* 2015) and to the present day (e.g. *Childonophora* Thomson, 1927). Unattached, cemented and encrusted lifestyles increased dramatically in the Ordovician with the emergence and rise of craniids, discinids and in particular the strophomenids (Harper *et al.* 2013, 2015). However, both lifestyles were already in place in the Cambrian, ecospace occupied by taxa such as *H. orienta* and *I. haikouensis* (Fig. 4). An interstitial life habit, comparable with Recent brachiopod *Gwynia* (Harper & Moran 1997) has been presumed for acrotretid brachiopods, one of the most widespread and abundant orders of brachiopods in the upper Cambrian and into the lower Ordovician

(Streng 1999; Holmer & Popov 2000; Topper *et al.* 2013b,c). This interpretation was exclusively based on their minute size, however, acrotretid specimens from Chengjiang Biota and the Burgess Shale Lagerstätte clearly show individuals attached to sponges and algae (Wang *et al.* 2012; Topper *et al.* 2015b). Their miniature size in this case an adaption to a suspended epifaunal, perhaps epiplanktic life style, similar to what has been suggested for the Cambrian coral-like tomteluvids (Brock 1999; Streng *et al.* 2016) and the Ordovician siphonotretid, *Acanthambonia* (Wright & Nõlvak 1997). It is possible though that acrotretids and other diminutive brachiopods had a number of different life strategies and as a meiofaunal lifestyle cannot be ruled, it is included here with some uncertainty. Ordovician protorthoids, such as *Skenidioides* and *Protoskenidioides* have also been interpreted as occupying an interstitial ecospace, however, this is also unclear and based solely on the small size of the shells (Waisfeld *et al.* 2003).

The major innovation regarding life strategies for brachiopods in the Ordovician is the evolution of an infaunal life habit. Both extant linguloid genera are infaunal burrowers (Thayer & Steele-Petrovic 1975) and this mode of life has been assumed for the majority of the fossil representatives of the group, including Cambrian members (Jin *et al.* 1993). However, evidence to support a burrowing behaviour is inconclusive (Pemberton & Kobluk 1978) and fundamental morphological distinctions support an epifaunal or semi-infaunal life habit (Zhang *et al.* 2005). Presently, *Leontiella* sp. represents the oldest burrowing linguloid taxon (Balinski & Sun 2013) and it seems likely that this transition from an epifaunal fixosessile lifestyle to a fully infaunal mode of life evolved between Cambrian Stage 5 (equating with the Burgess Shale) and the beginning of the Ordovician.

Despite the apparent fluidity in brachiopod lifestyles across the Cambrian-Ordovician transition, the brachiopod communities of the Ordovician were probably quite different from their Cambrian counterparts. The Great Ordovician Biodiversification Event (GOBE) is not only characterized by a remarkable increase in taxonomic diversity, but also in sheer biomass, biocomplexity and a striking increase in α diversity (Harper 2006, 2010). Individual assemblages increased from containing less than 10 species in the Late Cambrian to over 30 by the Late Ordovician, producing more densely packed communities (Harper 2006, 2010) and heightening competition as individuals sought for suitable attachment substrates for unimpeded growth and feeding (Tyler & Leighton 2011; Topper *et al.* 2015a,b). This increase in sheer biomass is immediately obvious when comparing the direct fossil evidence of brachiopods preserved in life position (Figs 1 and 2). Both Cambrian and Ordovician brachiopods display gregarious attachment strategies, however Cambrian clusters tend to be numerically reduced and substrates uncongested when compared to Ordovician attachment clusters. For example, the large majority of attached specimens in the Cambrian display a solitary lifestyle (Zhang & Holmer 2013; Topper *et al.* 2015a,b) and in terms of the maximum numbers of individuals attached to the same substrate, there are only five *M. burgessensis* individuals in the Burgess Shale community attached to *Tubulella* sp. (Topper *et al.* 2015b; Fig. 1A) and 18 individuals of *K. malungenesis* in the Chengjiang community attached to algae (Wang *et al.* 2012, fig. 2). These numbers pale in comparison to the 60 *Z. modesta* individuals using a crinoid for substrate (Sandy 1996), the 30 *Onniella* individuals attached to a bryozoan (Harper & Pickerill 1996) and the hundreds of orbiculoid brachiopods attached to orthocones in the Soom Shale (Gabbott 1999). The lack of suitable taphonomic conditions in the Ordovician probably accounts for the paucity of

brachiopods preserved in life position, however on the evidence available it appears that in Ordovician benthic communities, competition for suitable substrates for settlement had escalated.

In the vast majority of cases, these gregarious assemblages of attached brachiopods are conspecific clusters (Sandy 1996; Harper & Pickerill 1996; Gabbott 1999; Zhang & Holmer 2013; Topper *et al.* 2015b). In each case, a wide range of specimen sizes are present, from juvenile to adult (Sandy 1996; Harper & Pickerill 1996, fig. 3; Gabbott 1999, table 1; Topper *et al.* 2015b; Fig. 1A) and most likely represent a life assemblages with attached brachiopods settling from numerous spawning events. This begs the question as to whether 1) brachiopod larvae in the Cambrian and Ordovician possessed at least some degree of selectivity when searching for suitable settlement and attachment sites and/or 2) did adult brachiopods attract conspecific larvae to settle on or near them, possibly by use of some unknown chemoautotrophic signal (Crisp 1979). Preferential settlements of extant brachiopod larvae have been experimentally shown in laboratory conditions (Pennington *et al.* 1999) and settlement-inducing chemical cues have been suggested (Pennington *et al.* 199; Peck *et al.* 2001); however studies are too few to draw adequate conclusions. Regardless, conspecific, gregarious attachment strategies appear to have changed little since the group emerged in the Cambrian.

The information presented herein suggests that in terms of occupied ecospace, brachiopods have seen little expansion since the Cambrian. Waisfeld *et al*. (2003, fig. 4) recognized a similar trend in Ordovician assemblages in Argentina and proceeded by further subdividing the three guilds occupied by rhynchonelliform genera into eleven different lifestyles based on the wide range of shell morphologies present in the communities. The escalation of orthide and strophomenide brachiopods on the

Ordovician seafloor (Harper *et al.* 2013) is echoed in the emergence of a vast spectrum of morphologies (Harper 2004, 2006, 2010). Cambrian brachiopod communities on the other hand were dominated by linguliformean brachiopods, a group that is considered to have a relatively conservative morphological nature (Kowalewski *et al.* 1997; Topper *et al.* accepted). Despite not observing a significant increase of occupied ecospace (Fig. 3-4), it is possible that the advent of new shell shapes and morphologies allowed these life strategies to be adaptively fine-tuned, perhaps providing improved morphologies to deal with the onset of elevated competition and the exploration of new environments.

Conclusion

Brachiopods underwent an unprecedented hike in diversity and abundance in the Ordovician, however this radiation was not mirrored in an expansion of ecospace. Brachiopods in the Cambrian possessed a range of life strategies; pedicle attachment, pedicle anchoring, free lying and cementation and were predominantly low to medium level epifaunal tierers together with some semi-infaunal forms. The life strategies of Ordovician brachiopods were essentially the same; with the significant exception that linguloid stocks began to explore the infaunal realm. The density of brachiopods attached on the same substrate though increased immensely, suggesting increased competition for suitable attachment substrates in the Ordovician benthos. The reoccurrence of gregarious conspecific clusters sharing the same substrate insinuates that a mechanism, possessed either by the larvae and/or the adult form prompted larval settlement. The GOBE may record one of the greatest taxonomic diversifications in the history of the Brachiopoda, however the majority of life

strategies were already established, having evolved during the Cambrian. Perhaps analogous to the taxonomic expansion witnessed at lower systematic levels in the Ordovician, brachiopod life strategies that were established during the Cambrian may have underwent a similar subdivision, in order for groups to develop more opportunities and partition niches during the rise in α diversification experienced in the Ordovician.

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Figure captions

Figure 1. Life strategies of some Cambrian brachiopods. A-D from the Cambrian Series 3, Stage 5 Burgess Shale Lagerstätte. A, Five individuals of *Micromitra burgessensis* Resser, 1938 attached to *Tubulella*, arrow pointing towards juvenile, ROM63170, RQ+8.2. B, *M. burgessensis* attached to the sponge *Pirania*, ROM63187, BW-170 cm. C, the pedicle anchoring brachiopod, *Lingulella waptaensis* Walcott, 1924 with pedicle, ROM59324, Greater Phyllopod Bed. D, *Nisusia burgessensis* Walcott, 1924 attached to *Wiwaxia corrugata* (Matthew), ROM61116, BW-210 cm. E-J from the Cambrian Series 2, Stage 3 Chengjiang Lagerstätte. E, the pedicle anchoring brachiopod *Eoglossa chengjiangensis* Jin, Huo & Wang, 1993, ELI-BLICxx (004JS). F, the semi-infaunal anchored stem-group brachiopod *Yuganotheca elegans* Zhang et al. 2014, ELI-BLCxx. G, *Alisina* sp. attached to the exoskeleton of a trilobite, ELI-BO 001AB. H, the free-lying *Heliomedusa orienta* Sun & Hou, 1987, ELI-BO (JS0673A). I, *Inquilinus haikouensis* Han et al., 2004 cemented to the margin of *Diandongia pista* Rong, 1974, ELI-BD-005. J, the pedicle anchoring *Lingulellotreta malongensis* Rong, ELI-BO (0286B). All scale bars 5 mm.

Figure 2. Life strategies of some Ordovician brachiopods. A cluster of *Onniella* attached to a bryozoan. Block NBMG 9976 reposited in the New Brunswick Museum. Figure modified from Harper & Pickerill 1996, fig. 2.

Figure 3. The ecospace flat iron for brachiopods. Ecospace as defined by the three axes of tiering, attachment strategy and motility.

Figure 4. Modes of life utilized by Cambrian and Ordovician brachiopods. Black boxes are life strategies documented and reported in the text. Grey boxes are modes of life that seem plausible, however supporting evidence is tenuous.

Table 1. Basic ecological categories for tiering, attachment strategies and motility.